

The Origin of Platyrrhines: An Evaluation of the Antarctic Scenario and the Floating Island Model

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ABSTRACT This paper evaluates whether 1) protoplatyrrhines could have migrated to South America via Antarctica, and 2) the floating island model is a plausible transoceanic mode of dispersal for land vertebrates like protoplatyrrhines. Results show that Eocene Antarctica and Australia supported large and dense forests, and that the Antarctic fauna was comprised of many species of vertebrates, including placental and marsupial land mammals. However, no primate remains have ever been reported from these continents. Antarctica and South America were connected until the Middle Eocene (i.e., after the oldest Asian anthropoids), but two major water barriers existed between Antarctica and Asia since the Early Eocene. The Eocene and Oligocene water gap separating Africa and Antarctica was excessively large. Thus, all scenarios involving an Antarctic route have been rejected. The African scenario is difficult to falsify because only one water barrier existed, both paleowinds and paleocurrents were favorable, and Paleogene African anthropoids show phylogenetic affinities to platyrrhines. I tested whether a journey on a hypothetical floating island over the Paleogene Atlantic Ocean exceeds the survival limit of a genetically viable group of animals such as protoplatyrrhines. Studies of water deprivation suggest that they could have been able, with a body weight averaging 1 kg, to survive without water for at least 13 days. I have used the present Atlantic Ocean as a model for the velocity of Paleogene paleowinds and paleocurrents. Considering winds as the key accelerating force of floating islands, the Paleogene Atlantic water barrier could have been crossed, in the most conservative scenario, in 8 days at 50 Mya, 11 days at 40 Mya, and 15 days at 30 Mya. In order to survive a transoceanic journey, however, protoplatyrrhines had to be preadapted to strong seasonal variations in water availability in their original (African) environment. Once on the sea, their brains would have physiologically interpreted the rarity of water as the beginning of the dry season, and the group would have switched its diet to alternative foods, i.e., everything available on the floating island. *Am J Phys Anthropol* 109:541-549, 1999. © 1999 Wiley-Liss, Inc.

It has been proposed that platyrrhine ancestors originated in Africa or North America, and that their access to South America must be accounted for by fortuitous water dispersal (e.g., Ciochon and Chiarelli, 1980a; Fleagle, 1988, 1999), because South America was an island at times of migration

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(Tarling, 1980; Aiello, 1993; Houle, 1998; Fleagle, 1999). The rafting hypothesis was first suggested by Alfred Russell Wallace in the mid-19th century (Simons, 1976; Joki, 1990), and has been addressed to explain the origin of many organisms, notably the South American acridian insects (Amedegnato, 1993), West Indian Coleoptera (Nichols, 1988), Lake Malawi fishes (Oliver and McKaye, 1982), many shallow-water animals (Joki, 1990), some amphibians and reptiles (Estes and Baez, 1985; Buffetaut and Rage, 1993) including Crocodylia (Densmore and White, 1991), *Crotalus* rattlesnakes of Baja California (Stewart, 1990), land reptiles of Western Samoa (Gill, 1993), South American indigenous gekkos (Kluge, 1969), some land vertebrates of the Krakatau Islands (Rawlinson et al., 1990), land mammals of the Mediterranean islands (Schüle, 1993), South American caviomorph rodents (Lavocat, 1969, 1980; Wood, 1980; George, 1993), a group of Australian rodents (Simpson, 1953), and possibly a group of South American sloths (Storch, 1993).

Four recent discoveries are worth noting for their potential impact on debates of platyrrhine origins. First, the presence of Eocene anthropoids in Asia has been supported by a number of newly discovered fossils (Chaimanee et al., 1997; Beard et al., 1994, 1996; Ducrocq et al., 1995; MacPhee et al., 1995), opening the possibility that platyrrhines are descended from one of these groups. Second, an Early Oligocene rodent has been found in southern Chile (Wyss et al., 1993), suggesting that platyrrhine monkeys of this age could also be found at this high latitude. Third, a dry land connection existed between Patagonia and the Antarctic Peninsula until the Late Eocene (e.g., Barker et al., 1991), allowing transcontinental biotic exchanges. Finally, placental and marsupial land mammals were extracted from the Eocene Antarctic Peninsula. Some of them are related to South American taxa (e.g., Hooker, 1992). Taken together, these discoveries raise the question of whether platyrrhines are descended from an Asian group of anthropoids. Furthermore, whether they are Asian descendants or not, could protoplatyrrhines have accessed South

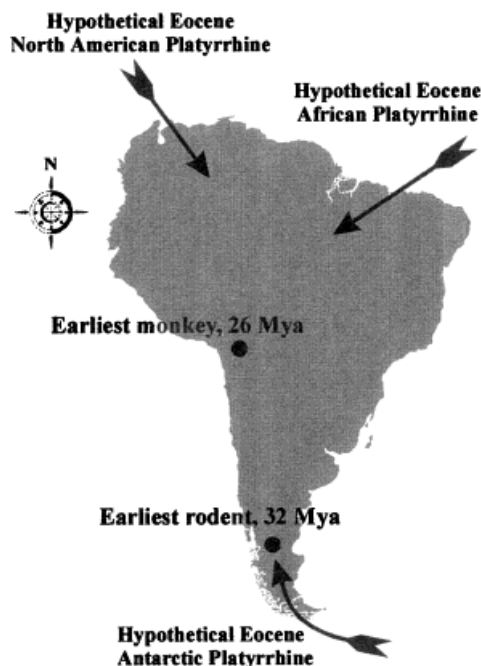


Fig. 1. Three paleobiogeographic scenarios of platyrrhine origins. Note the southern position of the earliest known rodent (Early Oligocene) compared to the earliest known platyrrhine (Late Oligocene).

America via Gondwanaland, by another migration route than the hypothesized trans-Atlantic or trans-Caribbean routes (Fig. 1).

In this paper, I evaluate two hypotheses. The first states that New World monkeys reached South America from Antarctica, i.e., from Asia and then via the Gondwanan continents (Asia ► Australia ► Antarctica and then ► South America) or from Africa (Africa ► Antarctica and then ► South America). This hypothesis of an Antarctic origin of platyrrhines once caught some attention (Fleagle, 1988; Ciochon and Chiarelli, 1980b), was eventually dismissed (Fleagle and Kay, 1997), and was then revived (Fleagle, 1999). The second hypothesis examines whether transoceanic migration on floating objects like a floating island is a plausible mode of dispersal for a group of animals such as protoplatyrrhine monkeys. This type of migration can be considered as feasible if it is demonstrated that such a journey does not temporally exceed the sur-

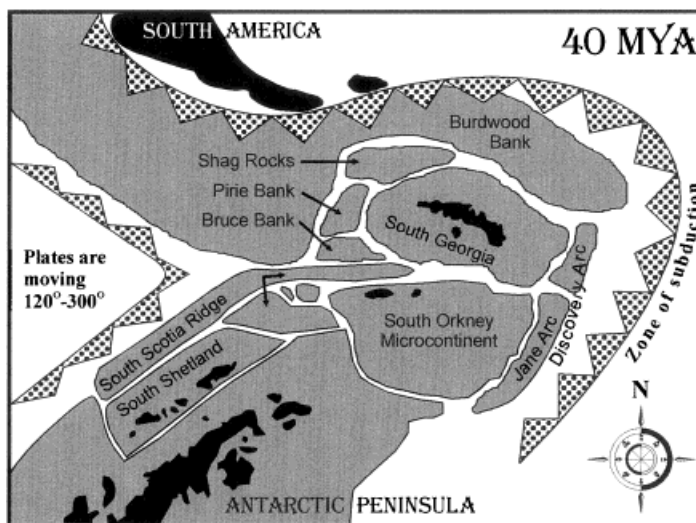


Fig. 2. Reconstruction of the Scotia Arc region at 40 Mya. Dark zones represent dry lands. After Barker et al. (1991).

vival limit of a genetically viable group of founders.

BACKGROUND

Antarctic migration scenarios

If protoplatyrrhines passed through Antarctica to reach South America, then four scenarios are possible. First, the oldest common ancestor of anthropoids was Asian, and one group migrated towards southeast Asia, Australia, and Antarctica, and then reached South America. Second, the oldest common anthropoid ancestor was African, and one group migrated towards Asia and then towards southeast Asia, Australia, Antarctica, and South America. In a third hypothesis, the oldest common anthropoid ancestor was still African, but one group migrated directly towards Antarctica (crossing the Southwest Indian Ocean) and then reached South America. Finally, the oldest common ancestor of anthropoids was North American, and one group migrated towards Asia (via the Bering Strait) and then respectively towards southeast Asia and Gondwanan landmasses.

Paleogene tectonic history of southeast Asia and Gondwanan continents

Reconstructing Paleogene tectonic history is important because it allows evaluation of the likelihood that the targeted continent could have been reached easily or not (i.e.,

whether major water barriers existed or not). The Scotia arc once connected the South American continent to the Antarctic Peninsula from 40 million years ago (Mya) to 10 Mya (Barker et al., 1991). The microcontinental fragments now dispersed within the region once formed a compact Antarctic-South American isthmus (Barker et al., 1991) (Fig. 2). The final separation of Patagonia and the Antarctic Peninsula (also known as the Opening of the Drake Passage) occurred during the Late Eocene, approximately 37 Mya (Barker et al., 1991; Toker et al., 1991). It allowed the passage of deeper water, leading to the formation of the Circum-Antarctic current. With cool water entering, a significant drop of air and water temperatures occurred (Denton et al., 1991; Veevers, 1984; Zinsmeister, 1982; Kemp, 1978), contributing to ice sheet development (Denton et al., 1991; Stanley, 1987). The planktonic composite suggests significant Antarctic ice volume during most of the Oligocene and Early Miocene (Denton et al., 1991). Paleobiogeographically, a land animal that could reach either of these two continents (South America or Antarctica) before 37 Mya had potential access to the other one.

Faunal and floral interplay between Antarctica and Australia could have terminated at magnetic anomaly 24 (~53 Mya: Paleogene geochronology from Berggren et al.,

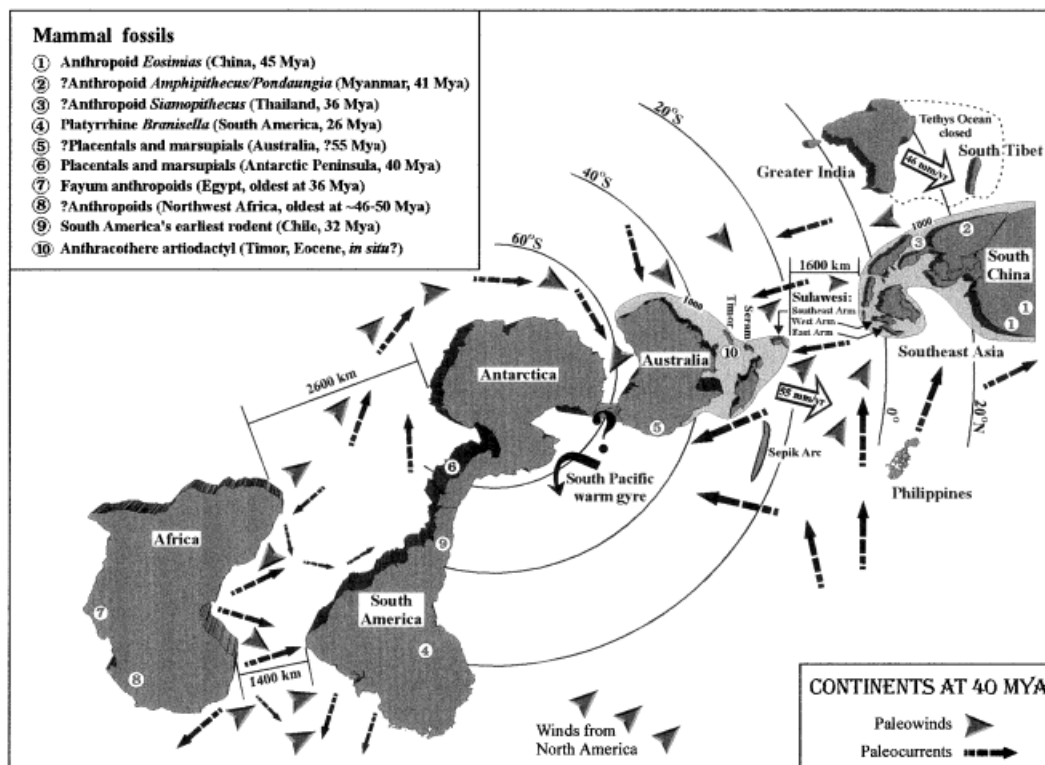


Fig. 3. Plate reconstruction of most of the world at 40 Mya, paleobiogeography of selected mammals, and direction of paleocurrents and paleowinds from that period of time.

1995), but Veevers (1984) reported that dispersal between the two blocks could have been maintained via the South Tasman Rise until perhaps as recently as 34 Mya, at the Eocene-Oligocene boundary (Fig. 3). More recently, however, Woodburne and Case (1996) presented evidence of an earlier separation of southeast Australia from Antarctica, at least by 50 Mya and possibly up to 64 Mya. At anomaly 19 (~42 Mya), the marine barrier between Antarctica and Australia was "at least 1000 km" (Woodburne and Case, 1996, p. 127). The paleobiogeographic significance of these data is that any land animal that could reach any of these three continents (South America-Antarctica-Australia) before the late Middle Eocene (Veevers, 1984) or before the late Early Eocene (Woodburne and Case, 1996) had potential access to the other two.

The collision of the Australian plate on southeast Asia happened in the Late

Miocene, 10.2 Mya (Lee and Lawver, 1994, 1995) or during the Middle Miocene, 15 Mya (Veevers, 1984). The distribution of island arcs between Eocene Australia and southeast Asia is unknown, but it is likely that the paleosea between the two regions contained some of them (Lee and Lawver, 1995; Hutchison, 1989). In the Early Eocene, 50 Mya, the distance between the northernmost tip of the Australian plate and the southernmost island of southeast Asia approximated 2,100 km (see maps in Lee and Lawver, 1995). In the Middle Eocene, 40 Mya, while Antarctica was still connected to South America but possibly not to Australia, the distance between the Australian plate and southeast Asia had decreased to 1,600 km (Fig. 3). In the Early Oligocene, 30 Mya, the leap was probably less than 1,000 km. In the Middle Eocene, 40 Mya, paleowinds were blowing north and currents were flowing south (Baron and Peterson, 1991) (Fig. 3).

Paleoenvironment of Antarctica and Australia

This section reviews the Paleogene environment of Antarctica and Australia. It is asked whether the environment of these two continents during the Paleogene could have supported a small arboreal protoplathyrhine, particularly on Antarctica. Floras on early Tertiary Antarctica clearly have much in common with those of Australia, New Zealand, New Guinea, and southern South America (Truswell, 1991). The flora in the Antarctic Peninsula was dominated during most of the Eocene by angiosperm trees, podocarp conifers, and araucarian conifers (Doktor et al., 1996; Woodburne and Case, 1996; Truswell, 1991; Case, 1988; Francis, 1986). Ferns and some angiospermous shrubs formed the subcanopy (Truswell, 1991). There were intensely seasonal conditions, and the majority of the angiosperm taxa were deciduous (Truswell, 1991). Angiosperm leaves greater than 10 cm long have been discovered on Alexander Island (Thomson and Burn, 1977). The large size of these leaves could be related to warm-temperate conditions. Eocene paleotemperatures on Seymour Island have been estimated to vary between 6–16°C (Porebski, 1995; Ditchfield et al., 1994; Sadler, 1988). The presence of well-marked growth rings in Antarctic woods illustrates that their growth environment was characterized by well-defined seasons (Francis, 1986). A heavy rainfall of perhaps 1,000–2,000 mm/year was assumed for the peninsula by Francis (1986). Ecologically, a land mammal could have survived in such paleoenvironmental and paleoclimatic conditions, although a specialized mode of life, specifically adapted to seasons with long hours of daylight during the summer and almost complete darkness during the winter, would have been necessary. The time of development of the Antarctic ice sheet is important because no land mammals, unless excessively specialized, can survive on continental glaciers. The onset of Antarctic glaciation has been estimated to date from the Late Eocene to Early Oligocene (Anderson, 1991; Denton et al., 1991; Truswell, 1991; Ditchfield et al., 1994). One of the lowest drops in sea level during the past 500

million years took place during the Early Oligocene (Haq et al., 1987). This lowest record in sea level temporally coincides with the final tectonic separation of the Antarctic Peninsula and Patagonia, the onset of the Circum-Antarctic current, and the appearance of glaciation in continental Antarctica. It seems unlikely that any terrestrial mammal, unless highly specialized, would have persisted for long on Antarctica after the late Eocene.

The Paleocene environment of southeastern Australia was characterized by conifer-dominated wet forests, while mesothermal rainforests prevailed in the interior (Woodburne and Case, 1996). In Early Eocene southeastern Australia and coastal Queensland, forests were dominated by diverse angiosperms and tropical mangroves. In the interior, communities showed strong ecological differentiation, with locally different dominant types. All Eocene forests are associated with global cooling from the Cretaceous to Early Miocene (Kemp, 1978; Deep Sea Drilling Project [DSDP] 277, 279, 281). Early Eocene paleotemperatures reached a comfortable 20°C, and rainfall was probably seasonal (Greenwood, 1996). However, an abrupt drop of temperature occurred in the latest Eocene (Kemp, 1978), which temporally coincides with the final tectonic separation of Antarctica and South America and the onset of the Circum-Antarctic current. No ecological constraint could have limited the survival of a land mammal like an arboreal protoplathyrhine on Australia before the Late Eocene.

Paleogene mammals of Antarctica and Australia

Many plant, invertebrate, and vertebrate fossils have been reported from Antarctica, although most of them were found on the Antarctic Peninsula, especially from Seymour Island (Fig. 4). Depositions on Seymour Island and surrounding islands occurred throughout the Campanian to the Eocene. Of particular significance is the discovery of the first Antarctic *placental* (Bond et al., 1989; Hooker, 1992; Marenssi et al., 1994) and *marsupial* (Woodburne and Zinsmeister, 1982, 1983, 1984; Case et al., 1988) land mammals on Seymour Island. Materials recovered include: 1) polydolopid

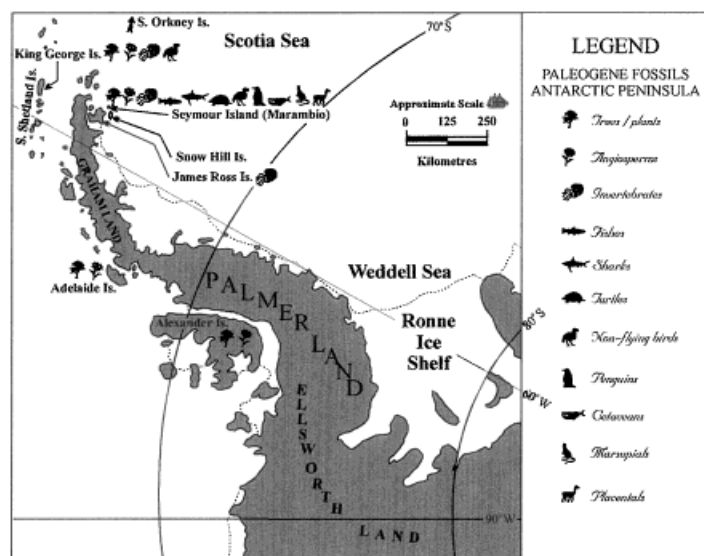


Fig. 4. The Antarctic Peninsula, its main locations, and Paleogene fossil sites. Note the presence of placental and marsupial mammals on Seymour Island.

marsupials, 2) microbiotheriid marsupials, 3) astropothere ungulates (the size of a tapir), 4) litoptern ungulates, 5) edentates, and 6) possibly a chiropteran (Woodburne and Case, 1996; Marenssi et al., 1994; Hooker, 1992; Colbert, 1991; Case et al., 1988). Associated marine invertebrate fossils indicate a late Middle Eocene age (Bartonian), about 40 Mya. This is approximately 3 Myr before the Drake Passage opened (cf. Barker et al., 1991). Associated fauna includes invertebrates such as echinoids, asteroids, crinoids, brachiopods, and crabs, and vertebrates such as sharks, teleost fishes, turtles and other reptiles, and whales, as well as birds such as penguins and ratites (Doktor et al., 1996; Aguirre-Urreta et al., 1995; Tambussi et al., 1994; Jerzumska and Swidnicki, 1992; Colbert, 1991; Young, 1991; Myrcha et al., 1990; Mitchell, 1989; Case et al., 1987; Woodburne and Zinsmeister, 1982, 1983, 1984; Covacevich and Rich, 1982; Zinsmeister, 1982). The discovery of *Antarctodolops dailyi*, a 20-cm-long polydolopid marsupial, is important because of its close relationship to the South American *Polydolops thomasi*, known in Paleocene and Eocene Argentina (Woodburne and Zinsmeister, 1982, 1983, 1984).

The oldest fossil mammals in Paleogene Australia were thought for a long time to be of Late Oligocene age, approximately 22

Mya (Tedford et al., 1975). More recently, fossil fauna at Murgon in southeastern Queensland, the Tingamarra local fauna, yielded an impressive array of Early Eocene fossils, including birds, frogs, snakes, turtles, bats, marsupials, and (maybe) land placentals (Godthelp et al., 1992). Radiometric dating has given a minimum age estimate of 54.6 Mya (Godthelp et al., 1992). The paleobiogeographic significance of this discovery is enormous. It means, if true, that Eocene *placentals* did reach Australia, and this discovery challenges the common presumption that marsupials dominated therian assemblages because of failure of placentals to access the Australian continent before the Late Tertiary (Godthelp et al., 1992). However, Woodburne and Case (1996) challenged the view that the Tingamarra local fauna at Murgon was of Early Eocene times, and presented evidence that *Tingamarra porterorum* is not a condylarth placental mammal, as proposed by Godthelp et al. (1992), but a marsupial of possibly Oligocene age.

The island-hopping hypothesis and the floating island model

Two modes of dispersal have been suggested to explain the distribution of land animals over large water barriers: island-hopping and rafting. Island-hopping is an

unlikely mode of dispersal over two continents separated by an oceanic gap. First, tropical large rivers and lakes with an access to the ocean are likely places of floating island growth, and these kinds of rivers and lakes are rarely found on small oceanic islands. Second, the chances that a floating island comes alongside a small volcanic island somewhere in a large ocean are excessively small. Third, genetically and evolutionarily, a *viable group* of animals must be present on the floating island when it departs from its main terrestrial base, an unlikely event in itself and most improbable when repetition from island to island is required. Moreover, islands were rare if not nonexistent in the Eocene Atlantic Ocean, a presence often assumed (cf. Fleagle, 1999; Holroyd and Maas, 1994; Aiello, 1993; Lavocat, 1993; Tarling, 1980) but rarely demonstrated. For instance, the Sierra Leone Rise was most probably below sea level during the Eocene, with a paleodepth of approximately 1,880 m (DSDP 366: Aubry, 1995), as was the Walvis Ridge, with a paleodepth of 1,500–2,200 m (DSDP 363: Aubry, 1995; Oberhänsli et al., 1991). Moreover, although one site (DSDP 526) located in the middle of the Walvis Ridge contained shallow-water organisms, these were dated Late Paleocene (Parrish, 1993). In the same way, Site 359, on the western end of the Walvis Ridge, might also have been exposed, but it was no later than 47 Mya (Parrish, 1993). The Falkland Plateau connection between South America and Africa was severed even earlier (at the Aptian-Albian boundary), as the southern South Atlantic opened before the northern South Atlantic (Parrish, 1993). Only the crest of the Rio Grande Rise might have been aired out by as late as the Oligocene (Parrish, 1993). No matter how low the sea water level was during the Oligocene (Fleagle, 1988, 1999; Hartwig, 1994; Aiello, 1993; all referring to Vail and Hartenbol, 1979, or Haq et al., 1987), these excessively rare islands along the South American coasts cannot explain the transoceanic migrations of platyrrhine monkeys, caviomorph rodents, and the other South American organisms noted above.

Rafting is an expression covering the dispersal of land organisms across water on

floating objects. Floating elements like islands, however, are more substantial in size than the word “raft” suggests (Darlington, 1957; Lavocat, 1993). Because any transoceanic journey on a small raft is unlikely for a genetically viable group of land animals the size of early platyrrhines, I shall refer to the mode of dispersal for this type of organisms as the *floating island model*.

The difficulty of transoceanic migrations depends on the characteristics of each particular organism (Tarling, 1980; Simons, 1976; Houle, 1998). There are many physical, physiological, and behavioral objections to any transoceanic journey for animals such as protoplatyrrhines (Simons, 1976; Houle, 1998). Despite these, there is still the small probability that, in the past: 1) a floating island developed, 2) a floating island detached from mainland, 3) a genetically viable primate group was on the island when it detached, 4) primates were not able to escape the moving island, 5) local paleocurrents and paleowinds transported the island to the ocean, 6) the floating island and primates on it survived oceanic storms, 7) most importantly, primates did not suffer from dehydration, 8) the vegetation on the island did not significantly wither due to salt spray and provided enough food for survival, 9) primates were able to withstand wind and heat stresses, 10) the island was favored by both oceanic paleocurrents and paleowinds and reached South America, 11) primates were alive upon arrival, and 12) they presented normal behaviors, were inclined to reproduce, and were able to adjust to the new environment (including new seasonality, new unfamiliar foods, new predators, new transmissible diseases, new parasites, etc.). Many of these objections, however, may be overcome if: 1) likely places of floating-island growth can be identified, 2) these regions included a likely center of origin of the taxonomic group, 3) the region was adjacent to both favorable oceanic paleocurrents and paleowinds (or else, paleowinds were powerful enough to compensate for unfavorable paleocurrents), and most importantly 4) *such a journey could have been completed within a reasonable number of days, i.e., within the survival limit of the migrating organisms*.

Although floating islands as a mode of dispersal have often been mentioned in the literature, they have been observed or described quite rarely (reviewed in Houle, 1998). For instance, a floating island impressive for its size was reported in Canada in 1881, drifting on a medium-sized river near Waterloo in the Province of Quebec (see Fig. 1 in Houle, 1998). This floating island later broke into smaller islands, and the largest measured approximately 60×23 m, with trees as high as 15 m (Hughes and Gaudet, 1967). This is the largest floating island ever recorded. Some floating islands were observed on lakes, and their growth and ecological parameters have been partially described (e.g., MacMillan, 1894; Trivedy et al., 1978).

Scheltema (1971) calculated that a minimum of 60 days and up to 400 days is actually necessary for *benthic* organisms to cross the Atlantic Ocean. Simons (1976), who attempted to parallel these data with transoceanic migration of terrestrial animals, rightly concluded that such a journey is much too long for primates such as platyrrhines. He concluded that lack of water and food, salt imbalance, and environmental stresses would render most small primates comatose or unconscious in 4–6 days. The problem with this analogy is that transportation by currents of very small marine animals like benthic organisms are not affected by surface winds. As we shall see, the wind (not the current) is the most powerful force on the ocean, and is probably the critical factor in the floating island's velocity.

METHODS

The Antarctic hypothesis must consider: 1) the number of water barriers (if any) that had to be crossed in a given scenario during the Paleogene, 2) the distance between a pair of continents separated by a water barrier, 3) the distribution of both paleocurrents and paleowinds during that period of time, and whether the circulation patterns were favorable or not to transoceanic dispersals, and 4) phylogenetic affinities between putative ancestors from the source continent and South American platyrrhines. A migration path separated by the least number of water barrier(s) is considered as the

most plausible. Likewise, a transoceanic migration has a greater chance of success when the distance between two lands is smallest, and when both paleowinds and paleocurrents are favorable. The Antarctic migration route is contrasted with the African and North American hypotheses, and the scenario which least contradicts each of these four variables will be considered the most parsimonious.

The second hypothesis evaluates whether transoceanic dispersal (floating island model, rafting, and island-hopping) is a plausible mode of migration. The ultimate objective is to estimate the number of days needed by a floating island to cross the Paleogene Atlantic Ocean (50, 40, and 30 Mya), and tests whether such a journey exceeded the survival limit of a genetically viable group of animals such as platyrrhine ancestors. Resistance to water deprivation appears to increase with body weight among mammals (four species tested; data from Cortes et al., 1988). For instance, *Octodon degus*, a Chilean rodent with a mean body weight of 210 g (Silva and Downing, 1995), can survive up to 13.4 days without water, while the smaller 31-g (Silva and Downing, 1995), sympatric *Oryzomys longicaudatus* can survive only 4 days in total water deprivation conditions (Cortes et al., 1988). Assuming that proto-platyrrhines had a body weight averaging 1 kg (Ford and Davis, 1992), the floating island hypothesis will not be rejected (and will be considered plausible) if it can be demonstrated that the transoceanic journey on a hypothesized floating island did not exceed 13 days.

In order to test the floating island hypothesis, one needs the circulation patterns of both paleocurrents and paleowinds, the paleodistance separating two continents at each time period, and the velocity of a hypothetical floating object. Although paleowind and paleocurrent *circulation patterns* have been modeled for the Paleogene oceans, their *velocity* is unknown. I used the present Atlantic Ocean as a model. One critical aspect of this plan is the fact that *paleodistances* and *ancient* circulation patterns of currents and winds have been involved in

TABLE 1. Evaluation of four different paleobiogeographic scenarios of platyrrhine origins¹

	AFR ► SAM	AFR ► ANT ► SAM	ASIA ► GON ► SAM	NAM ► SAM
Water barrier (number)	Pro (1)	Pro (1)	Con (2)	Pro (1)
Water barrier (length in km)	Pro (1,400)	Con (2,600)	Pro (<1,000 and 1,600)	Pro (<1,000)
Paleocurrents	Pro	Con	Pro	Con
Paleowinds	Pro	Pro	Con	Con
Phylogenetic affinities	Pro	Pro	Pro?	Con

¹AFR, Africa; SAM, South America; ANT, Antarctica; GON, Gondwana; NAM, North America; ►, migration to. Number of water barriers, scenario with the largest number of water barriers considered least. Length of water barriers, scenario with the largest distance considered least. Paleocurrents, scenarios considered likely if paleocurrents were flowing towards the targeted continent. Paleowinds, scenarios considered likely if paleowinds were blowing towards the targeted continent. Phylogenetic affinities, likely if a taxonomic group, putative ancestor of platyrrhines, was present on the source continent.

calculations with *present* velocities of currents and winds. This of course raises the question of how modern winds and currents describe velocity patterns in the past. Until these parameters are set, however, one is restricted to alternatives. Current and wind velocity of the Atlantic Ocean have been collected from modern marine pilot charts (Defense Mapping Agency, 1994, 1995). Two areas in which currents flow continuously westwards, i.e., without loops, backloops, and tropical doldrums, have been sampled. From these areas, only cells (5° of latitude by 5° of longitude) in which dominant winds (known as trade winds) blow from east to west, i.e., in the same direction as currents, were retained. This context simulates a *continuous path* along which a floating object would have the highest chance to cross the ocean. Sampling a region dominated by doldrums and backlooping currents, for instance, would have been useless. Indeed, it is well-known to experienced sailors that floating objects can be caught for weeks in these regions (sailors Jean Malouin, Josée Péloquin, and Lieutenant Christian Drolet, personal communication, 1998). Pilot charts of the Caribbean Sea and the southeast Indian Ocean were also consulted, but currents in these regions do not flow as continuously as in the modern Atlantic Ocean because of the presence of many archipelagoes. Modern pilot charts of the Pacific could not be obtained. As mentioned above, there are two regions in the Atlantic Ocean where both currents and winds are *simultaneously* favorable to transoceanic migration. One (between 5° North to 10° South) originates near the Congo River in the Democratic Republic of Congo, and currents there flow toward the Paraíba, Amapá, and Maranhão

States in Brazil. The other (between 10° North to 30° North) is located just north of the Senegal River in Senegal; currents there flow toward northern Brazil and Venezuela. Marine maps produce a rich set of information, notably on current velocity and direction, wind velocity, wind direction and their associated frequencies, the distribution of wave height and their respective frequencies, mean air temperatures, air pressure, and so on. Data on marine charts are now recorded monthly, allowing examination of seasonal changes of winds and currents. Wind velocity is defined by navigators on a 12-unit scale, known as the Beaufort scale (Defense Mapping Agency Hydrographic-Topographic Center, 1995; Watney, 1980). A wind of Force 0 has a mean velocity of less than 1 knot (the surface of the sea is described as a mirror; 1 knot = 1.852 km/hr); Force 1 has a mean velocity of 2 knots; Force 2, a mean of 5 knots; Force (F) 3, 9 knots; F4, 13 knots; F5, 19 knots; F6, 24 knots; F7, 30 knots; F8, 37 knots; F9, 44 knots; F10, 52 knots; F11, 60 knots; and F12, above 65 knots (a hurricane).

RESULTS

Evaluation of scenarios

Results summarizing the Antarctic migration hypothesis (and other postulated migration routes) are summarized in Table 1. Geophysics data do not support the hypothesis of a land migration from Asia to South America via the Gondwanan landmasses after 50 Mya, if not 64 Mya (cf. Woodburne and Case, 1996). Indeed, if one major water barrier existed at 60 Mya (between southern Southeast Asia and the north of the Australian Plate), probably two barriers were pre-

sent at both 50 and 40 Mya (the preceding barrier plus the channel between Australia and Antarctica). At 37 Mya, South America, Antarctica, Australia, and Southeast Asia were isolated from each other until the Australian Plate collided with Southeast Asia in the Middle to Late Miocene. An African origin followed by an Antarctic migration must also be rejected. Indeed, if only one water barrier was slowing down the migration (the Paleogene southwest Indian Ocean), this barrier was excessively large (Fig. 3). The paleoenvironments of Eocene Antarctica and Australia were suitable for small to medium-sized mammals, and this element does not help in the falsification of any Gondwanan scenario. Phylogenetically, although both placentals and marsupials have been recovered from the Eocene Antarctic Peninsula, their presence in Eocene Australia is still debated, and no rodent or primate remains have ever been recovered on the Antarctic Peninsula, even in the rich fossiliferous beds of Seymour Island (Sergio Marensi, personal communication, 1998). Rejection of all scenarios involving an Antarctic migration route is recommended. Africa is phylogenetically the most likely source of early platyrrhines (Fleagle, 1999), and only African transoceanic dispersals were favored by *both* paleocurrents and paleowinds (cf. Barron and Peterson, 1991; and see below). The African migration is considered the most parsimonious hypothesis (*sensu* Fleagle, 1999). However, concluding that protoplatyrrhines arose in Africa and migrated directly to South America via the Atlantic Ocean does not explain *how* platyrrhine ancestors could have survived a transoceanic journey. This is a crucial question, and the next section tests its feasibility.

Currents and winds of the present Atlantic Ocean

A sample of westward currents for each month of the year was collected in two areas of the south Atlantic Ocean, one between 5° North to 10° South ($n = 252$; Table 2), and the other between 10° North to 30° North ($n = 386$; Table 2). Figure 5 illustrates the dominant current in each 5° square of longitude and latitude of the sampled area. Currents in the southern area flow from the

Congo River in the Democratic Republic of Congo to the Paraíba, Amapá, and Maranhão States in Brazil. In the northern area, currents flow from the Senegal River in Senegal (and slightly north of it) to northern Brazil and Venezuela.

The month of July in the southern area is the month with fastest current velocity (1.25 knots; 1 knot = 1.852 km/hr), and October in the northern area, the slowest (0.574 knots). Differences between months are important in the southern area (Kruskal-Wallis analysis of variance (ANOVA), $H_{adj} = 55.58$, $P < 0.001$), but not in the northern area ($H_{adj} = 8.11$, $P = 0.703$). Overall, current velocity ranges monthly from 1.1–2.3 km/hr in the present south Atlantic Ocean.

Wind data were obtained from the same areas covered for currents (Table 2; Fig. 5). There is a significant seasonal effect in wind force in both the southern area (Kruskal-Wallis; $n = 443$; $H_{adj} = 24.58$; $P = 0.011$) and the northern area ($n = 350$; $H_{adj} = 27.3$; $P = 0.004$). The month of January in the northern area produced the fastest winds, with a mean force of 4.2 (approximately 26 km/hr), and the month of March in the southern area is the slowest, with a mean force of 3.5 (approximately 20 km/hr). The variability in wind force is smaller in the northern than the southern region (Table 2) (Houle, 1998). The northern winds are more powerful than the southern winds (Kolmogorov-Smirnov; $n_1 = 350$, $n_2 = 443$; $z = 4.434$; $P < 0.001$). Overall, monthly values of wind velocity vary little (though significantly), from approximately 20–26 km/hr. A global mean force of 3.84, which corresponds to approximately 12.4 knots or 23 km/hr, is computed when all wind values are pooled ($n = 793$).

The direction of winds varies from one place to another, within the same day and month, and between the seasons. There is, however, a clear dominance in wind direction in both surveyed regions (see Houle, 1998 for a descriptions of these winds). The issue here is that most of these winds are favorable for westward transoceanic migrations, particularly when they are examined concurrently with currents, and thus one can assume that present conditions are rep-

TABLE 2. Velocity of westward currents (in knots) and winds (in Force on the Beaufort scale) for each month of the year in two areas of the present south Atlantic Ocean, one between 5° North to 10° South, the other between 10° North to 30° North¹

Westward current velocity in knots from Africa to South America												
Month	5° North to 10° South						10° North to 30° North					
	n	Mean	Minimum	Maximum	SD	Variance	n	Mean	Minimum	Maximum	SD	Variance
January	21	0.824	0.4	2.0	0.351	0.123	41	0.646	0.3	1.5	0.268	0.072
February	21	0.805	0.4	2.0	0.363	0.131	43	0.642	0.2	1.4	0.259	0.067
March	21	0.743	0.4	2.0	0.346	0.120	31	0.587	0.4	1.2	0.235	0.055
April	21	0.786	0.4	2.0	0.393	0.154	22	0.645	0.4	1.1	0.230	0.053
May	21	0.805	0.4	2.0	0.388	0.150	38	0.697	0.4	1.5	0.311	0.097
June	21	1.186	0.5	2.2	0.428	0.183	31	0.665	0.4	1.7	0.304	0.092
July	21	1.252	0.5	2.2	0.457	0.209	37	0.624	0.4	1.1	0.215	0.046
August	21	1.186	0.5	2.2	0.446	0.199	29	0.614	0.4	1.1	0.207	0.043
September	21	0.876	0.5	1.9	0.367	0.135	35	0.620	0.4	1.3	0.191	0.036
October	21	0.871	0.5	1.9	0.358	0.128	27	0.574	0.4	1.0	0.170	0.029
November	21	0.881	0.5	1.9	0.353	0.125	30	0.630	0.4	1.2	0.193	0.037
December	21	0.84	0.4	2.0	0.35	0.121	22	0.627	0.4	1.3	0.227	0.052
All months	252	0.92	0.4	2.2	0.41	0.171	386	0.633	0.2	1.7	0.240	0.058

Wind velocity in Force (Beaufort scale) from Africa to South America												
Month	5° North to 10° South						10° North to 30° North					
	n	Mean	Minimum	Maximum	SD	Variance	n	Mean	Minimum	Maximum	SD	Variance
January	36	3.58	3	4	0.5	0.25	33	4.15	4	5	0.36	0.133
February	39	3.54	3	4	0.51	0.255	32	4.06	4	5	0.25	0.06
March	38	3.45	3	4	0.5	0.254	33	4.06	4	5	0.24	0.059
April	36	3.58	3	4	0.5	0.25	30	4.00	4	4	0.00	0.00
May	35	3.8	3	4	0.41	0.165	27	4.00	4	4	0.00	0.00
June	41	3.76	3	4	0.44	0.189	29	4.03	4	5	0.19	0.034
July	37	3.78	3	5	0.48	0.23	29	4.03	4	5	0.19	0.034
August	37	3.76	3	5	0.55	0.3	26	4.00	4	4	0.00	0.00
September	34	3.71	3	4	0.46	0.214	25	3.92	3	4	0.28	0.077
October	35	3.71	3	4	0.46	0.21	25	4.00	4	4	0.00	0.00
November	37	3.81	3	4	0.4	0.158	28	4.00	4	4	0.00	0.00
December	38	3.74	3	4	0.45	0.199	33	4.00	4	4	0.00	0.00
All months	443	3.68	3	5	0.48	0.23	350	4.03	3	5	0.19	0.037

¹ Data from Defense Mapping Agency (1994, 1995). One knot equals 1.852 km/hr. See last paragraph of Methods for a description of the Beaufort scale of wind velocity. Each wind rose of the pilot chart presents the distribution of winds that have prevailed over a considerable period of time in series of 5° squares of longitude and latitude. Wind information on charts includes: 1) the direction from which the wind blew (every 45°), 2) frequencies of observations (wind dominance), 3) the average Force of winds on the Beaufort scale, and 4) the percentage of calms. Wave heights in both sampled regions were among the lowest in the south Atlantic Ocean (less than 10% were higher than 4 m). Currents near the shore of the South American continent were the most rapid. Backlooping currents and currents going towards backloops were ignored. Only dominant winds (frequencies of at least 30% in each 5° square) were sampled. The surveyed regions are illustrated in Figure 5.

representative of those during the Eocene (compare the marine pilot charts published by the Defense Mapping Agency (1994, 1995) with the model by Barron and Peterson (1991) of Paleogene paleowinds and paleocurrents).

The effect of wind on floating islands

The effect of wind on floating islands is complex to evaluate. Among the factors to consider, there are wind velocity and direction, current velocity and direction, the positive effect of wind on the crowns of trees and all other organic and inorganic materials, the size and mass of the island, the degree of buoyancy of the entire floating mass, the

negative effect of water resistance on the submerged base of the island, and so on. Until all these parameters are understood, the effect of wind on the velocity of a floating island will be estimated as follows. Because water resistance on the submerged base of the island is probably important (increasingly important as the velocity of the island increases), and because winds do not always blow optimally, the efficiency of the *additive* effect of wind (as a pulling force) is assumed not to exceed 25% (Paul Guimond, engineer, and Jean Malouin, sailor, personal communication, 1998). In other words, three quarters of wind energy are lost because of these two limitations. Therefore, the velocity v of an

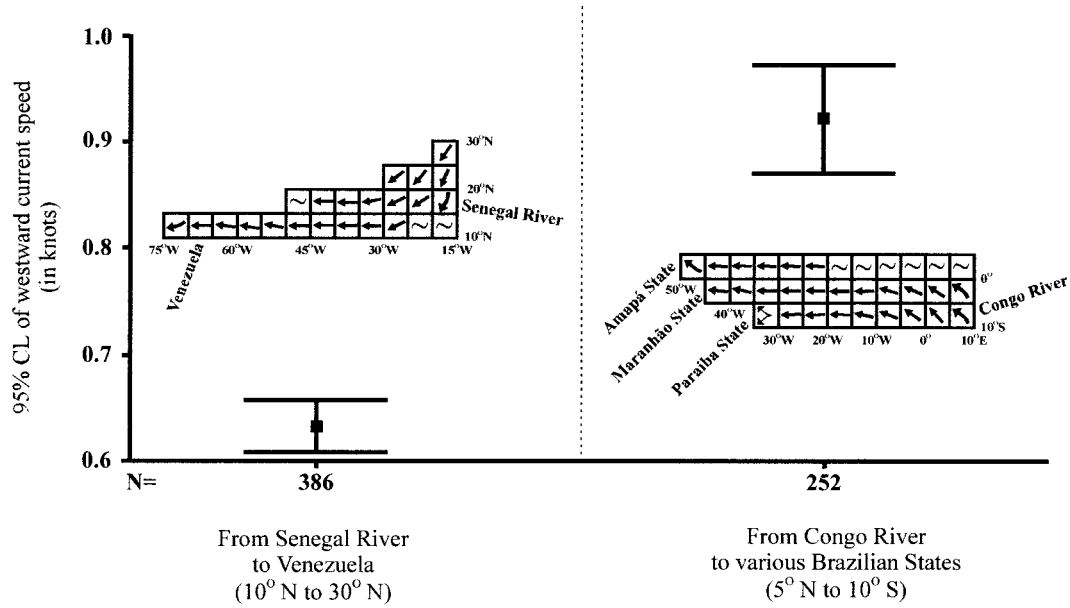


Fig. 5. Confidence limits (CL, 95%) of current speeds in two regions of the present Atlantic Ocean. Also shown are the dominant current in each 5° square of longitude and the latitude in which the velocity of currents and winds was sampled. ~, seasonal variations in currents direction. Both areas were chosen because currents and winds are actually favorable to westward transoceanic migrations (a simulation of past conditions). After Houle (1998).

object in this context is equal to:

$$\frac{\text{stronger force} - \text{weaker force}}{4} \pm \text{weaker force}, \quad (1)$$

where the term to the left represents the additive effect of the stronger force on the object's velocity. The equation should then be translated for our purpose into

$$v = \frac{w - c}{4} \pm c, \quad (2)$$

where w is the wind velocity and c the current velocity. The term to the left represents the additive effect of wind on the floating island's velocity, and the term to the right is added or subtracted (the \pm symbol), depending on whether paleocurrents were flowing in the same (addition) or in the opposite (subtraction) direction than paleowinds were blowing. If time is equal to the distance divided by the velocity, then the number of days δ to cross a water barrier is

equal to:

$$\delta = \frac{\text{distance (km)}}{\text{floating island velocity (km/h)}} \div 24. \quad (3)$$

Before going any further, a comment about oceanic paleodistances must be addressed. The *shortest* paleodistance between two continents is not representative of the real distance that has to be crossed, because currents never flow in straight lines. Rather, currents follow slight curves, at least in the present Atlantic Ocean (Defense Mapping Agency, 1994, 1995). In order to resolve this bias, a correction factor has been added to various paleodistances, which will be called *sailing* paleodistances (see Houle, 1998). Overall, the number of days needed by a floating island to cross an ancient water barrier can be calculated as follows:

$$\delta = \frac{\text{sailing paleodistance}}{\frac{w - c}{4} \pm c} \div 24. \quad (4)$$

TABLE 3. Estimated number of days for a hypothesized Paleogene floating island to cross the south Atlantic Ocean at 50, 40, and 30 Mya¹

Currents velocity (knots)	Number of days to cross the Paleogene South Atlantic (winds effect ignored)		
	50 Mya	40 Mya	30 Mya
1.252 knots (fastest currents, July)	19.3	27.0	36.6
0.747 knots (mean currents, all months)	32.3	45.2	61.4
0.574 knots (slowest currents, October)	42.0	58.8	79.8
Sailing paleodistance in km	1,072.0	1,501.0	2,037.0
Wind Force (Beaufort scale) and currents velocity (knots)	Number of days to cross the Paleogene South Atlantic (additive effect of winds)		
	50 Mya	40 Mya	30 Mya
F4.152/1.252 knots (fastest winds/currents)	5.2	7.3	10.0
F3.835/0.747 knots (mean winds/currents)	6.8	9.5	12.9
F3.447/0.574 knots (slowest winds/currents)	7.7	10.8	14.7
Sailing paleodistance in km	1,072.0	1,501.0	2,037.0

¹Above: winds effect ignored; below: wind effect added. "Sailing paleodistance" is a corrected "shortest paleodistance" that takes into account curved paths of currents (cf. Houle, 1998). In the lower part, the number of days to cross the Paleogene south Atlantic Ocean has been calculated using Equation (4). Note the discrepancy of results whether the effect of wind is considered or not in calculations.

Table 3 summarizes the results. In the upper part of Table 3, the effect of wind has been ignored, and only current velocity has been used in calculations. In the lower part of Table 3, calculations have incorporated the additive effect of winds, using Equation (4). Considering the *mean* velocity of currents concurrently with the *mean* velocity of wind (Table 3), the Paleogene journey could have been made in 7 days at 50 Mya, 10 days at 40 Mya, and 13 days at 30 Mya. However, the same paleodistance could have been covered in only 5 days at 50 Mya, 7 days at 40 Mya, and 10 days at 30 Mya if the month in *fastest* current velocity of both regions is computed with the month in *fastest* wind speed. In the most conservative scenario, when the month in *slowest* current velocity is computed concurrently with the month in *slowest* wind velocity, the Paleogene water barrier could have been crossed in 8 days at 50 Mya, 11 days at 40 Mya, and 15 days at 30 Mya. Table 3 shows that the effect of winds is crucial on the velocity of a floating

island, as values are almost 5 times higher when winds are ignored. The floating island hypothesis is not rejected and is considered as plausible for a Paleogene transoceanic migration of platyrrhine ancestors.

DISCUSSION

The Antarctic migration route and the origin of platyrrhines

Four biogeographic scenarios are associated with a hypothesized Antarctic origin of platyrrhines. The evidence *compatible* with (but not necessarily supportive of) these scenarios can be summarized as follows. First, the fauna and flora on Eocene Antarctica are more abundant and diversified than previously thought (Woodburne and Case, 1996; Marenssi et al., 1994; Hooker, 1992; Colbert, 1991; Francis, 1986, 1991; Truswell, 1991; Webb, 1991; Young, 1991; Myrcha et al., 1990; Mitchell, 1989; Case, 1988; Case et al., 1987, 1988; Zastawniak et al., 1985; Woodburne and Zinsmeister, 1982, 1983, 1984; Jefferson, 1983; Covacevich and Rich, 1982; Kemp, 1978; Thomson and Burn, 1977). Second, a land bridge between South America and Antarctica probably existed until the late Middle Eocene (Barker et al., 1991), i.e., after the appearance of the oldest Asian anthropoid (Beard et al., 1994, 1996). Third, the Eocene paleoenvironment on Antarctica and Australia was cool to warm-temperate, and both continents supported large and dense forests (Antarctica: Ditchfield et al., 1994; Gazdzicki et al., 1992; Francis, 1986, 1991; Truswell, 1991; Webb, 1991; Case, 1988; Zastawniak et al., 1985; Jefferson, 1983; Kemp, 1978; Thomson and Burn, 1977; Australia: Alley et al., 1996; Greenwood, 1996; Woodburne and Case, 1996; Carpenter and Pole, 1995; Scriven et al., 1995; Hutchison, 1989; Veevers, 1984; Kemp, 1978). Fourth, Eocene communities of faunal affinities with South America existed on both Antarctica and Australia, strongly supporting the long-suspected Gondwanaland migration exchange (Woodburne and Case, 1996; Marenssi et al., 1994). The Eocene Antarctic fauna included placental and marsupial land mammals and many other animals (Godthelp et al., 1992). The evidence *against* the hypothesis of an Antarctic

tic origin of platyrrhines is threefold. First, if a water barrier really existed between Australia and Antarctica during Eocene times (Woodburne and Case, 1996), then any land migration from Asia to South America would have required a journey over *two* major water barriers, a difficult hypothesis to sustain. Second, Eocene paleowinds between southeast Asia and Australia were not favorable (Barron and Peterson, 1991) (Fig. 3). Finally, no primate fossils have ever been recovered on the Antarctic Peninsula (S. Marensi, personal communication, 1998), even in the rich fossiliferous beds of Seymour Island. Considering the present evidence, the Antarctic hypothesis is not supported.

Paleontological evidence does not support a North American origin (Fleagle, 1999; Fleagle and Kay, 1994, 1997; Holroyd and Maas, 1994; Ciochon and Chiarelli, 1980b; Delson and Rosenberger, 1980). Additionally, both paleowinds and paleocurrents were not favorable for transoceanic migration (Barron and Peterson, 1991), and this hypothesis has essentially been abandoned (Fleagle, 1999). The African origin is the most difficult hypothesis to falsify (Table 1) (Fleagle, 1999; Fleagle and Kay, 1997; Hartwig, 1994; Holroyd and Maas, 1994; Aiello, 1993; Ciochon and Chiarelli, 1980a). Only one water barrier had to be crossed, the distance between the continents was reasonably small for a transoceanic migration (Fig. 3), and both paleowinds and paleocurrents were concurrently favorable (Barron and Peterson 1991). Phylogenetic affinities among Paleogene Fayum anthropoids and platyrrhines also support the African hypothesis (Fleagle, 1999). If one considers that the oldest known platyrrhine monkey fossil, *Branisella*, is rather young (Late Oligocene, ~25.5 Mya; Takai and Anaya, 1996) compared to the oldest African anthropoids of Eocene age (Late Eocene, ~36 Mya; Simons, 1995; Kappelman, 1992; Kappelman et al., 1992), and if one assumes that platyrrhine primates and caviomorph rodents arrived in South America roughly simultaneously, then the discovery of the 32 Myr rodent in the central Chilean Andes provides an opportunity for discovery of

platyrrhine monkeys significantly older than those presently known (Wyss et al., 1993).

The floating island model and platyrrhine origins

Table 3 presents the minimum, maximum, and mean number of days that were necessary for a hypothesized floating island to cross westerly the Paleogene south Atlantic Ocean. It also shows how significant the additive effect of winds is on the velocity of a floating island, since wind is a much stronger force than current (Table 2). Models revealed that at 30 Mya, the Oligocene Atlantic could have been crossed in 10–15 days. At 40 Mya, the Eocene ocean could have been crossed in only 7–11 days. Assuming that protoplatyrrhines arrived in South America during the Late Eocene or Early Oligocene (Fleagle, 1999), the present analysis suggests that the ancestors of New World monkeys were able to make the journey if they could survive at least a week. The fact that the level of sea water was particularly low during the Oligocene (cf. Haq et al., 1987) only contributed to shorten paleodistances separating the South American and African tectonic landmasses (exposed continental margins).

Simons (1976) underestimated the plausibility of transoceanic dispersals. He concluded that a group of protoplatyrrhines could survive without food and water for no more than 4–6 days. In fact, resistance to lack of water and nutritional resources varies greatly among mammals and reptiles (discussed in Houle, 1998). As mentioned above, tolerance to water deprivation appears to increase with body size among mammals. Assuming that protoplatyrrhines had a body weight averaging 1 kg (Ford and Davis, 1992), considering the scenarios presented in the lower part of Table 3, and taking into account how large a floating island can be (see Fig. 1 in Houle, 1998) and that it can provide significant amount of nutritional resources, transoceanic migrations might not be as spectacular and improbable as mentioned in the paleoprimateological literature. Moreover, animals experimentally exposed to water deprivation returned to their normal physiological values very rapidly, in fact in proportion to

the elapsed time of deprivation (Hossaini-Hilali et al., 1994; Ben Goumi et al., 1993). Studies have also shown that mammals living in xeric conditions are more adapted to endure water deprivation than those living in mesic environments (Freudenberger and Hume, 1993; Chilcott et al., 1985; Silanikove, 1985). These studies strongly suggest that protoplatyrrhines, in order to survive a transoceanic journey, were preadapted to strong seasonal variations in water availability. Once on the sea, their brains physiologically would interpret the rarity of water as the beginning of the dry season (and the group would switch its diet to alternative foods, i.e., everything available on the floating island). Another indication that suggests a seasonality of water in the environment of protoplatyrrhines comes from the fact that floating islands need a lot of water in order to grow (e.g., see the ecological descriptions of floating islands and their growth in Oliver and McKaye, 1982; Trivedy et al., 1978; Brewster, 1924; Powers, 1911; MacMillan, 1894). A mat of vegetation usually grows out from the shore, and only an important rise in water (a flood) can normally break off the network of densely tangled roots from the shelf, thus forming a floating island (Powers, 1911).

Some researchers have proposed that "as few as four trans-Atlantic colonizations over as much as 45 Myr might explain much of the South American placental fauna" (my emphasis; Sarich and Cronin, 1980, p. 419). Likewise, the Hoffstetter-Lavocat hypothesis of both caviomorph and platyrrhine origins involves *two* crossings of the south Atlantic (Wood, 1993). As discussed above, however, the success of Paleogene trans-Atlantic colonizations was less related to the duration of the journey or to the survival limit of the genetically viable group of monkeys, but more to other conditions related to the raft itself (e.g., the growth of a floating island near the shore of an ocean, the presence of animals on the island when it departed from the river bank, favorable paleocurrents and especially paleowinds at times of departure, and the floating island reaching South America). When all these conditions are grouped into one single event, its unlikelihood increases rapidly. If these condi-

tions must be repeated several times to explain several trans-Atlantic colonizations, then the improbability grows multiplicatively. The point here is that n taxa are more likely to migrate at the same time on the same floating island than n groups migrating separately. Considering the origins of caviomorph rodents and platyrrhine monkeys, for example, it is logical to postulate that both groups (with other animals and plants) made the trans-Atlantic journey on the same large floating island, and touched the coast of the New World on the same day. Areas where floating islands are produced might be rare, but when one exists, it can produce floating islands by the *hundreds* (Oliver and McKaye, 1982). This question cannot thus be resolved.

In summary, among all available scenarios of platyrrhine origins, the Antarctic or Gondwanan paleogeographic model is among the least probable, and has been discarded. Data of multiple sources support the hypothesis of a Paleogene African origin of New World monkeys. The group has phylogenetic affinities with Eocene/Oligocene African taxa, and paleocurrents and especially paleowinds between Africa and South America were favorable for a trans-Atlantic migration. Moreover, models using the velocity of winds and currents from the present Atlantic Ocean suggest that such a journey could have been made within a reasonable number of days, i.e., within the survival limit of animals like protoplatyrrhines, between a strict minimum of 7 days at 40 Mya to a maximum of 15 days at 30 Mya. One surprise in the present analysis is the slight variation in the length of any journey within a given period of time (lower part of Table 3). This is in high contrast with scenarios that ignored the effect of winds (compare the upper and lower parts of Table 3). Simons (1976) underestimated the likelihood of transoceanic dispersal of monkeys because he based his analogy on the migration of marine benthic organisms (cf. Scheltema, 1971), i.e., animals that simply follow the flow of currents. Up to 80% of a floating island is exposed to pulling winds (Houle, 1988). It seems that paleocurrents are not good indicators of potential transoceanic dispersals. Paleowinds, at least in the case of protoplat-

pyrrhines and their traveling companions, made the difference.

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